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Mitchell's Theorem

Roger Carolin

(John Ray Herbarium, University of Sydney)

Once upon a time there was a natural philosopher who came from one of the most barbaric states of Europe, inhabited so they said by witches and red-haired blue-eyed bandits. He had argued with famous men, taught students who one day would be more famous than himself, and at last arrived at the furthest confines of the civilized world. Although this description probably fits me so far, there are two significant differences. This man lived more than 2 millenia ago and he had a revelation whilst walking the shores of the great grass sea of central Asia. It was this: Life is not a series of disconnected beginnings and ends as his Greek friends thought, nor is it a ghastly circle that needs to be broken to bring blessed relief as thought his Indian friends. No, everything is in flux, one thing leads to another in a chain of inexorable change; a breathtaking vision in its infinity. This man's speculations, for they were really little else being based upon a very meagre data base, were taken up by people like John Dalton, Erasmus Darwin and Jean de Lamarck 2000 years later and provided the basis for much of modern science.

It is all very well to recognise that all is in flux but what determines the direction of that flux? In particular, from our point of view the flux of life? Charles Darwin seems to have provided an acceptable answer to that question in 1859. But then another arose immediately. When we cannot observe forms of life originating how can we determine which form gave rise to which form, or, better expressed, how can we determine the precise relationships of species? The systematists of the 19th century thought they had the answer: it was likeness. Affinities (relationships) were determined by characteristics held in common, and indeed wasn't it systems based on general likeness that had provided the inductive basis for the theory of evolution?

Many thought that some characters were more important than others and Lamarck and de Candolle argued about the method to be adopted in this "subordination". Indeed some features are more important than others. Let us examine that proposition. Consider three taxa with one attribute which can occur in two states 0 and 1. Assume they are derived from the same ancestor; assume state one arises only once; assume that state 1 having arisen, cannot revert to state 0. Assume the taxa do not cross. If the states are distributed as shown in Fig.1, there is only one phylogeny than can be accepted. By placing B on the A line we require separate origins of state 1 or reversion to state 0.

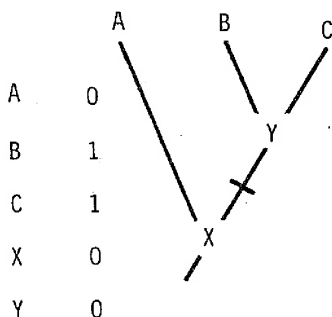


Fig. 1

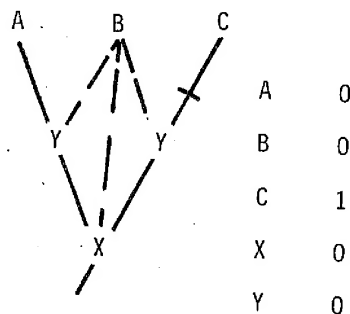


Fig. 2

To show that only advanced characters define cladogenesis: character states for one character shown, line on diagram shows position of change from 0 to 1.

If states are distributed as shown in Fig. 2 there are three possible phylogenies and three possible sequences of branchings. Only by using advanced character states or characters can we resolve branching sequences in phylogeny.

Julian Huxley coined the word "clade" for a taxon including a unit and its descendants. Subsequently modified to include all the descendants, the clades are monophyletic in Hennig's sense. Cladistics are concerned with the recognition of these clades, the recognition of the order of cladogenesis and thus the recognition of sister-groups or sister-clades. If this is the aim there is no escaping the method outlined above. It is comparable to a Euclidean theorem, if you accept the axioms the rest follows.

Mitchell set it out quite clearly in 1901, albeit in the discursive style of the early years of the century. Indeed, it is with a certain Anglo-Celtic arrogance that I call this talk Mitchell's Theorem. In fact, not 20 years after the publication of the "Origin of Species", Haeckel had established the principle. Both authors, particularly Mitchell, thought that the method was in general use although a perusal of the then current systematic literature shows that this was not the case. Since it is so clear, what is all the fuss about? As we do with Pythagoras' Theorem or The Bridge of Asses, why do we not learn it, use it in our daily lives and thank god that he made life so simple.

Indeed it is rather remarkable that it was not until 1950 that Hennig launched the theorem on a reluctant biological world in "Grundzuge einer Theorie der Phylogenetische Systematik". Feyerabend has described the propaganda and the repudiation of contradicting facts that is almost acceptable practice in the formulation of new scientific concepts. Suffice it to say that Hennig's proclamation of the new systematics was in the classical tradition. He even conscripted words into his service and gave them new meanings; in many cases, to be sure, more precise ones. Such has been his achievement that his concepts cannot be ignored although many do not accept them.

I have talked about phylogeny and strictly what I've drawn in the figures is a phylogenetic tree with ancestors included. However, there are other phylogenies that fit the facts as shown in Fig. 1 and Fig. 3 illustrates these.

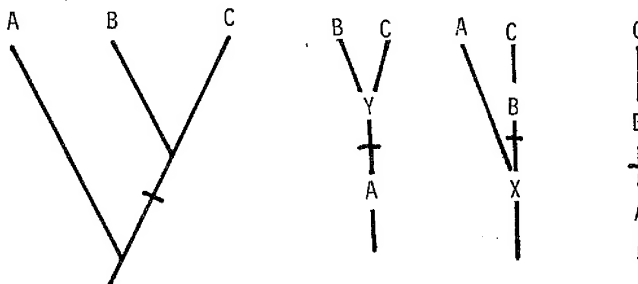


Fig. 3. Cladogram of phylogeny shown in Fig. 1 on left, other phylogenies for same cladogram to the right.

So we need to distinguish between a cladogram which is a tree depicting an order of origin of advanced characters and a phylogenetic tree which is a tree depicting ancestor-descendant relationships. The cladogram examines cladogenesis, the phylogenetic tree also examines anagenesis, that is the development of clades once they have arisen.

Were we to dispense with the root of the cladogram we have an undirected tree (Fig. 4) for dispensing with the root means being undecided about which state of the attributes concerned is primitive and which is advanced. What we have is a network showing character state differences between taxa. It has no time dimension and is usually referred to as a Wagner network.

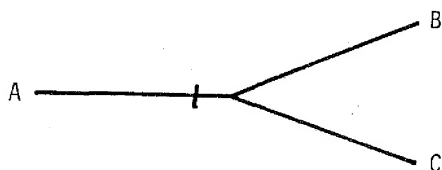


Fig. 4. Undirected Wagner tree (network).

The Wagner network, like most dendograms based upon overall similarity, is atemporal. But in a cladogram the attribute states have to be polarised, that is they are arranged in a series and one end of the series functions as a starting point. This polarisation must be related to some dimension. When attribute states are polarised as simple to advanced, a time sequence is implied. A cladogram is an order of origin of advanced states and therefore there is a time dimension although it is a scrambled metric as Orloci so charmingly calls it. And in the derived phylogenetic tree the time sequence is quite explicit, if not measured.

Until now we have met few problems. However here we do. How do we polarise character states? How do we determine what is advanced and what is primitive? Possibly the most frequent of the alternative states found in the group being analysed could be considered the most primitive. It seems hardly necessary to argue against this concept, but it is surprising how frequent it has been used. There is, of course, no reason why a change to an advanced condition should not occur near the base of a phylogenetic tree. The fossil record is a doubtful aid since we have no evidence on what did not occur in a particular stratum, only an incomplete record of what did. Likewise the method based upon correlation of characters, as used by Sporne, is not entirely satisfactory since correlation of advanced characters may also occur. Methods have been suggested for rooting undirected trees based on molecular data such as amino acid sequences in proteins, which assume a constant rate of change - something that cannot be assumed for the morphological features.

The most common method used is known as "outgroup comparison". This consists of taking a taxon which is closely related to the group being analysed and determining its position on the network, i.e., the taxon most like it in the tree. Thus the tree is given a direction, a root, and the characters are polarised. There are practical problems in doing this. Sometimes each character is taken separately and its status assessed in the outgroup and thus each character is polarised separately. Whatever the method, a sister group to the one under consideration has to be found for a reasonable result. But without a higher order cladogram this sister out-group cannot be defined; we have thus entered what is virtually an infinite regress. Thus outgroup comparison, strictly, fails! In fact what we usually do is to take the taxon which is assessed to be most similar by a higher order (phenetic) classification as the outgroup in the hope that it is at least close to the sister outgroup if, indeed, it is not it!

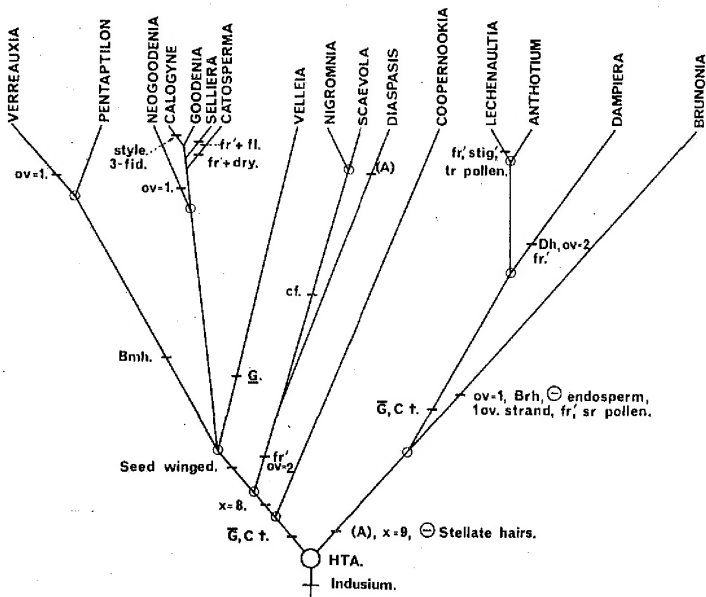
We may, of course, be prepared to polarise the character states on a priori developmental or functional grounds but that path is equally fraught with danger. None of this, of course, is exclusive to the cladistic method. It is general practice in phylogenetic studies although I believe cladistics have clarified the problems.

Although Hennig polarised character states before constructing cladograms, it is common practice now to construct a Wagner network and then polarise the character states.

An equally difficult problem confronts us in the construction of the cladogram. What happens when different characters give different cladograms, and thus, how can we construct a cladogram using these different characters? The attributes are then not congruent. Reversals to primitive conditions or separate origins (homoplasies) occur in the combined cladogram. The assumptions we made for Mitchell's Theorem are violated.

Well if we do get incongruent attributes we had better make sure that incongruencies are not due to our confusion. Such as confusing different character states under the same one, e.g., the petals we've called simply blue may be produced by different pigments in different taxa. We should make certain that the homologies we have recognised are in fact homologies. Indeed a standard procedure in systematics.

And let me say that I use homology here in the sense of equivalence and that homologous states can arise in separate lineages. I do not want to quarrel on word ownership but simply state it here so that there is no confusion.



Attribute state changes are indicated on the tree where they are presumed to have occurred as follows: *ov* = ovule number; (*D*) = connate anthers; *x* = basic chromosome number; \ominus = loss of; *Brh* = Brunonia hairs; *Dh* = dendritic hairs; *Bmh* = branched multicellular hairs; *f'* = indehiscent fruit; *stig'* = modified stigma; *tr pollen* = tetrad pollen; *sr pollen* = pollen with sextine ridges; *Cf* = Corolla fanned; \overline{G} = superior ovary; \overline{G} = inferior ovary; *Ct* = Corolla slit.

Fig. 5. Cladogram of the family Goodeniaceae. (reproduced with permission from Brunonia vol. 1).

To take a specific example. The cladogram of Goodeniaceae (Fig. 5) shows that the ovary position is incongruent with all other features in the case of *Velleia*, in which there is a reversion to a superior ovary. Examination of the ovaries of the clades lower in the cladogram show that the upper part of the ovary, which is unilocular, is always free from the androperianth. It is this upper part of the ovary which is developed in *Velleia* (Fig. 6) thus giving it the appearance of a superior ovary. Thus the cladistic analysis will detect possible errors in interpretation. So also, incidentally, could more intuitive methods but not, I think, so frequently or so clearly. Furthermore, the separate origins of the ovary in the *Dampiera* and *Goodenia-Scaevola* lines respectively indicates that they may not be homologous and my own studies on the vasculature of the ovary has shown this to be indeed so.

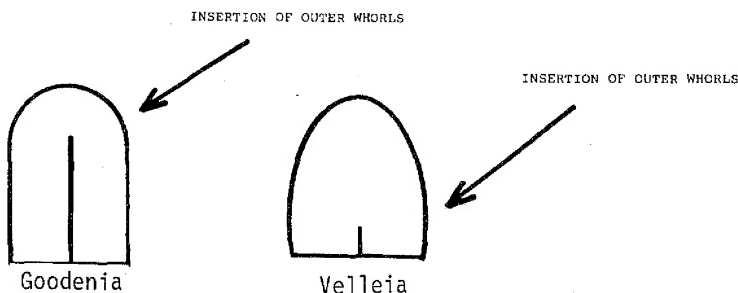


Fig. 6. Diagrammatic longitudinal section of ovaries of *Goodenia* and *Velleia*.

But what if no such errors come to light? At this point we enter a seeming morass created by a quiet medieval cleric from the gentle county of Surrey in the south of England. When William of Occam first wielded his razor, his intention was to solve disputations. The fact that it started an intense disputation itself does not detract from the service it has done mankind from an entirely pragmatic point of view. Paraphrased into modern jargon it means that to explain a particular phenomena, the smallest number of hypotheses necessary must be used.

In fact from a group of 9 taxa we can generate over 2,000,000 trees and from 10 taxa over 34,000,000! If we decide to accept the axioms promulgated above, this number is considerably reduced. If we do accept them and all the attributes are congruent then the cladogram (tree) necessarily becomes the tree with the least number of total evolutionary changes. Taking this principle to the case where the attributes are not congruent, can we not accept this as our criterion by which to choose the tree to be our cladogram?

Can we accept the cladogram with the least number of evolutionary changes, i.e. the most parsimonious one, to generate further hypotheses or as some people think as an hypothesis itself? This allows for as many reversals or separate origins as are necessary to obtain a most parsimonious cladogram.

It is, of course, a case of the use of Occam's razor. Overall parsimony minimizes the hypotheses needed to explain homoplasies. All methods for constructing trees are based upon parsimony although certain restrictions may be placed on the principle, e.g. reversals and/or separate origins may be

restricted or disallowed. Some methods assume constant and equal evolution rates and thus use other measures such as the sum of the lengths from each terminating taxon to the ancestor, but these are not really defensible at the morphological level.

Such, however, is the pristine purity of overall parsimony that it has proved fatally attractive. One wonders at times if one is not wielding Alexander's sword rather than Occam's razor.

Let us first be clear that there may be more than one parsimonious cladogram, and indeed unless we construct all the cladograms possible we cannot be sure that we have found it or them anyway. The problem here may well be NP-complete, as the mathematicians say.

Uncertainty is still lurking in our minds and judgement is still required. Of course one can always discard all those attributes which are not congruent and accept all those that are and thus build a cladogram. In effect we must find the largest group of compatible attributes and use this group - a collection which is given the unfortunate name of "clique". This is the basis of the character compatibility method. To some extent all phylogenists, even those who espouse overall parsimony, do this by discarding those attributes which they think may not be compatible, e.g. leaf size, plant size.

This problem of discarding characters from the analysis is only the extreme case of weighting characters, that is, character subordination. Many workers, once they have discarded characters, often for the same intuitive reasons for which they castigate others who weight characters in other ways, treat all characters in the same way. This seems illogical to me, if one is happy to give a weight of 0, one should bite the bullet and give other characters positive weighting when one thinks that it is necessary. The subordination might be done a posteriori by reducing the contribution of incongruent characters in some way or other or it may be done a priori e.g., by considering developmental implications.

Moreover, the nodes on a cladogram do seem to imply to me that combinations of character states at that point occur or occurred in a taxon. Should some of these states be functionally incompatible there may be good reasons for rejecting a "most parsimonious" cladogram which implies them in favour of a less parsimonious one excluding them. Unfortunately the history of biology is littered with the discovery of what were thought to be functionally impossible combinations from the duck-billed platypus onwards and although this is a valid reason for rejection, one must be most careful. Also, do not let us forget that several states of a character can exist in a taxon at one time and any one of the internodes or nodes can be polymorphic for several characters! Functionally incompatible states can co-exist in a population without actually occurring together in a viable organism. Our view on this will be coloured by the model of species and speciation which we are prepared to accept.

Possibly the complexity of characters might be a reason for subordination. But then we should ask: Are, in fact, the attribute states really single evolutionary novelties; are some of them not several evolutionary novelties combined? E.g. in Portulacaceae, at first sight, there is a clear binary distinction in the fruit; one in which the capsule has a single wall and dehisces through the 2-4 valves in the usual way: the other which has an epicarp which is deciduous, an endocarp which persists and 3(4) bristles which stand between the valves of the epicarp. But, when the fruits of the rarer genera are carefully examined, we can see that there are the following evolutionary novelties which can be apportioned to a number of attributes:

Capsule wall: undifferentiated
differentiated
Epicarp: dividing from endocarp
not dividing from endocarp
Epicarp: persistent
deciduous
Intervalvular strands: splitting in the middle
separating from rest of
ovary wall but remaining whole.

This, of course, is simply adjusting the cladogram in the light of new information and possibly complexity can always be analysed into separate valid characters.

Having made such adjustments, however, there may still be the possibility that a parsimonious cladogram violates parsimony in another aspect of biology, e.g. with regard to physiological or biochemical aspects of the morphological changes and their integration with other characters.

A value judgement is always involved, and, of course, might be wrong. It seems more satisfactory to me to make such judgements when one thinks they are necessary than not to make them at all.

You will notice that I am not rejecting parsimony as a criterion but I am saying that parsimony on the cladogram is not the only consideration.

Parsimony is in fact the only working rule that makes science possibly.

Evolution is essentially a series of events at the specific (or population) level; species give rise to other species. And although I am not going to define a species, I think you all know what I mean by it. Thus Rensch's classic "Evolution above the species level" is strictly speaking a nonsense title. All cladograms that depict cladistic analysis of a group of taxa above the category of species are even more symbolic than those depicting species. Indeed although Hennig and the earlier workers in the field were strictly concerned with the order of branching of sister-groups, cladograms above the species level show the order of origin of advanced characters. They are therefore fraught with danger if we do not exercise care.

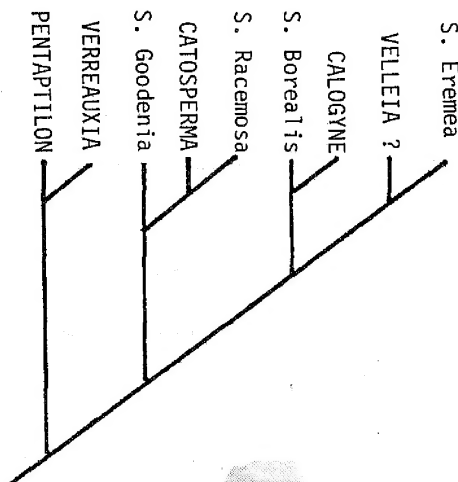


Fig. 7. Cladogram of Goodenia sections and some related genera.

For example in the *Goodenia* group of genera, the group of attributes that separate effectively the genera close to *Goodenia* can be used for cladistic analysis. Let us ignore those attributes which vary in the taxa under consideration such as hair type, habit etc. as we often do (Fig. 5). A nice clear cladogram results although not resolved into dichotomies in places (Fig. 7).

Now if we include all the species together in the analysis rather than lumping them into accepted genera, and use some of the attributes that vary throughout *Goodenia*, the result is quite different.

Indeed, in the case of *Calogyne* we can accurately define a sister-group within sect. *Borealis*, an undescribed species from Arnhem Land. This problem is not ignored in more orthodox systematics since we find someone writing that one taxon is close to another particularly to a certain part of the first.

The diagram of the *Goodenia* group raises another problem.

Hennig's maxim that only monophyletic groups, and that is groups which include the ancestor and all its descendants, should be recognised as taxa, clearly makes nonsense of genera like *Goodenia*. Several avenues are open to us in cases like *Goodenia*. *Goodenia* might be enlarged to include *Calyogone*, *Catosperma* and *Velleia*, or we might split *Goodenia* into several separate genera. *Goodenia* then is paraphyletic at present. That is compared with *Calogyne* it is defined by a primitive state, the unbranched style. Polyphyletic taxa, incidentally, are those grouped together on the basis of separately derived advanced characters.

We should also note here that probably every taxon at some time in its history becomes paraphyletic. We need to be careful about our Universe of Discourse and its division into operational units. Genera are man-made conveniences; species just may be much the same but they do mean more biologically speaking. Cladograms based on genera and above may not display cladistic relationships properly.

Hennig and his followers (cladists) would not accept paraphyletic taxa; others sometimes defined as evolutionary systematists, would do so. The terms cladist and evolutionary systematist are not particularly satisfactory in this context.

Possibly this displays the crux of the argument between these two schools of systematics at present; that is recognition of paraphyletic taxa. This means that anagenesis must be taken into account as well as cladogenesis. To the cladist the branching pattern of cladogenesis is a (testable) hypothesis of sequential changes, anagenesis provides no such hypothesis, indeed does not even provide an hypothesis about rates of evolution and is therefore untestable and largely irrelevant.

I hope that I have not overstated the cladists case or for that matter understated the evolutionists case, for like the Thracian refugee whom I described some minutes ago I hold an even more heterodox view, although I do not expect it to triumph in the way that the atomic theory or the theory of change did! System is our servant, it has two main functions, heuristic and information storage. It has other possibly less important ones, an aid to memory and an aid to identification. In many ways these demands are irreconcilable; Linnaeus recognised that and produced two systems at least, one heuristic and the other to cover the other functions. De Candolle recognised that but took no notice of it and after that every one tried to perform all except the last function with the one system.

It is clear though that when one is dealing with historic processes such as changes in the earth's environment and relating it to the historic processes of evolution, then we must use a system based upon clades, indeed based upon cladistic analysis. This does seem to me to be less speculative than evolutionary systems which nominate ancestors and which use anagenesis to generate hypotheses.

This does not mean that our nomenclature necessarily has to follow our clades. Again, names have several functions to perform and at least two of these are in conflict. As we refine our system the clades become more clearly defined (and become changed) which means that their nomenclature changes; names are used to describe our refinable system. But they are also memory addresses for information retrieval and changes in terms of this function are undesirable. Each case must be resolved as pragmatically as possible.

Let us remember that many other things show the same characteristics as organisms i.e. evolutionary change, such as pottery, any cultural artifacts in fact, language, ideas and so on. All can be dealt with in a cladistic analysis if it is thought it can generate useful hypotheses. Cladistic analysis is hypothesis generating.

Much of what I have said is applicable to any phylogenetic study and this merely points up that cladistic analysis has all the same problems that most of us try to cope with. Its basic tenets are the most satisfactory for developing phylogenetic hypotheses but they do need adjusting in the light of evidence.

It was all summed up long ago - almost back in the days of Democritus - when that other well-known thief and philosopher, my mother, said to me one bright blue day whilst I was helping her steal rose cuttings from King George VI's garden at Hampton Court: "You know, they're marvellous, they're always making new flowers and they know exactly how it happens". But that, of course, is another story!

THE WAGNER OLYMPICS: SHORT IS BEAUTIFUL.

Donald H. Colless,
Division of Entomology,
CSIRO, Canberra

The history of numerical cladistics shows an overall similarity to that of numerical phenetics. Both commence with the discovery that certain basic principles of systematics can be embodied in numerical algorithms; from this develops the notion that some aspect of biological 'truth' can now be accurately deduced from any reasonably good set of data. This attractive idea then spreads rapidly through a population of relatively unsophisticated 'true believers'; but eventually the dream fades. It turns out that numerical methods may provide answers that are multiple and conflicting, or for other reasons unsatisfactory. In other words, they generate hypotheses rather than conclusions. Their role lies in exploration, not revelation.

This historical parallel between numerical cladistics and numerical phenetics is not surprising, because there is no fundamental distinction between the two. To understand this, we must first understand the plain fact that, in normal usage, 'cladistics' may refer to three different things. First, and very roughly, it refers to the process of ordering taxa on a dendrogram, using various methods, but with this in common: the branching pattern may be interpreted as a reconstructed phylogeny of the group. Second, it refers to the use, when constructing a phylogeny, of inferences as to which states of a character are primitive and which derived. And third, it refers to the process of forming a classification that reflects the topology of a phylogenetic dendrogram AND NOTHING MORE. For instance, the classifier is forbidden to consider patristic distances on the tree or (anathema!) phenetic distances!

Insofar as cladistics uses numerical methods, it concerns itself almost exclusively with the first process (above), and takes little or no account of the second. This may come as a shock to some, but numerical cladistics is only marginally and indirectly concerned with the polarity of characters. Numerical processes are used primarily to derive what is in fact an undirected network. It becomes the familiar 'tree' only when a root is determined and placed on it. There, polarity of characters may and usually does come into play; but the primary algorithm has by then done its work and gone home. For instance, you may include in the OTU's a taxon bearing what you believe to be all the ancestral character states; and its position on the network will then automatically indicate the preferred root, according to your picture of the ancestor. But the algorithm neither knows or cares; your 'ancestor' is just another OTU that happens to be present. The zero's, one's, two's, etc. in your data table are merely symbols to be manipulated. They may be *ordered*; but it is immaterial in which direction the order runs!

I make this point because I find that it is often overlooked or misunderstood. And once understood, it becomes clearer that numerical phenetics and cladistics are overlapping subsets of a single body of computational theory. In various ways, they generate trees that are purely mathematical objects: with a topology, rooted or unrooted, and usually with lengths (weights) on the branches and/or character-values on the nodes. Having such a tree, we may then *interpret* it in various ways. For instance, a Wagner tree (Colless 1983) can be viewed as the most economical way to change any one OTU (terminal node) on a simply connected network into

each of the others by single-step changes along the branches - as it were, a "topological mean" of overall, phenetic distances. Alternatively, it has its well-known phylogenetic interpretation. A rooted Wagner tree can also be regarded as displaying 'special' similarities (Farris, 1979), in just those attributes that are 'novel'; i.e., inferred or hypothesised to be lacking on the node that represents the root. This is the 'transformed cladism' of, e.g., Platnick (1979), in which evolutionary theory has no relevance. In passing: I find it very hard to distinguish transformed cladism from phenetics; but perhaps it earns its title via the third usage (above): its practitioners seem to insist that taxa should be 'monophyletic' on the cladogram.

From now on I shall be dealing with numerical cladistics in the sense explicated above: the computation of unrooted trees interpretable as optimal estimates of phylogeny. Its history has many strands, but I shall concentrate on just one: the development of the Wagner method, principally by J.S. Farris. Its formal beginnings can be ascribed to the seminal papers by Farris (1970) and Farris et al (1970). The first demonstrated practical methods for estimating Wagner trees. The second formally translated Hennigian principles into the notion of a minimum-length tree; and, in passing, it is interesting that we find little or no trace there of one principle that was clearly treasured by Hennig himself: that of 'reciprocal illumination'. Something approximating to it could, perhaps, be injected by a differential weighting of characters, based on their complexity or any other feature that might express the confidence that we should place in them. However, no one seems to have tried to develop a rationale for such weighting, and very few programmes make provision for it.

In the paper by Farris et al (1970) we also find clearly stated the notion that 'actual choice of a phyletic tree [may be] left to an algorithm that effectively constructs the evolutionary hypothesis most in accord with available data'. And in Farris (1973) we find a spirited attempt to *prove* that the Wagner tree is indeed the maximum likelihood estimate of an evolutionary tree on the data. It is extremely important to realise what is being claimed there: that, once we are satisfied that our data are 'good', we can feed them to a computer programme and, in due course, receive back a firm conclusion that has been *logically deduced* from our data. However, for those who adopt this attitude, three problems now arise. Felsenstein (1981) has shown that the maximum likelihood interpretation holds true for a Wagner tree only under conditions that some might consider unrealistic. Under other conditions other techniques may claim maximum likelihood; but, having mentioned that point, I shall now have to ignore it. The second problem is strictly practical: as numbers of OTU's increase (currently, above 15 or so) it becomes impossible to test whether one has a genuine Wagner tree - i.e., one of actual minimum length. The relevant algorithms are heuristic, not rigorous - and, for some data sets, the 'Wagner algorithm' may be logically incapable of finding a Wagner tree! The third problem - actually, a group of problems - concerns the possibility that more than one Wagner tree may exist; or there may be many trees that differ so slightly in length as to require equal consideration in practice. How, then, should we seek the truth amongst such alternatives?

I will stress again that these problems relate essentially to the notion that the Wagner tree (or some other *logical* reconstruction) will *reveal* to us the *correct* interpretation of our data. Such a belief, combined with difficulties in recognising a genuine Wagner tree, can then generate what I have referred to in my title as the 'Wagner Olympics'. A set of data comes to be analysed over and over, perhaps using various techniques, in search of the ultimate, minimum-length tree. In practice much the same kind of contest can stem simply from attempts to develop improved techniques. The phenomenon itself is of little interest, but its results can be interesting. As a practical example, I shall discuss a set of 24 data matrices that are rapidly becoming

classical. They were introduced into methodological studies by Mickevich (1978) and have been most clearly described by Rohlf et al (1983b). Table 1 shows the lengths of the estimated Wagner trees found by a series of techniques and/or workers over the last 6 years. All techniques involved some version of the basic 'Wagner algorithm', but there were considerable differences in its application. Details are as follows:

- (a) Mickevich (1978). Stated to be a version of the Farris (1972) Distance Wagner algorithm, followed by branch-swapping, with lengths tested by Farris optimisation (Farris 1970). Some details are unclear, and some lengths seem to be erroneous (see discussion in Rohlf et al 1983b). Numbers 5, 18, 20, and 24 from the top seem unlikely to be strictly comparable with those from other methods.
- (b) Wagner 78. Farris' pioneer technique of that name, as employed by Rohlf et al (1983a,b).
- (c) Rohlf et al, A. The RWAG and SWAG programmes of Colless (1983), as employed by Rohlf et al (1983a).
- (d) Rohlf et al, B. The same, but with more extensive use of RWAG (Rohlf et al 1983b).
- (e) Swofford. Swofford's WAGPROC and PAUP programmes (Rohlf et al 1983b, Addendum); only new lengths were reported.
- (f) NWAG+. A programme NWAG (which consolidates Colless' RWAG, SWAG, and NINWAG as options, along with automatic optimisation), followed by local and/or global branch-swapping (programme NSWAP).

The first point to note is the steady improvement in techniques, both as regards the lengths of trees and the numbers of shortest trees found. Two well-known packages are not included: Felsenstein's PHYLIB and Farris' PHYSIS. I have no access to the latter, and I gather that the former is generally outperformed by the Swofford package, which is very attractive. With some data sets, it has given shorter trees than has any other programme in the table - although it should be noted that NWAG+ has outperformed Swofford's on occasion. That is mainly because my package allows the option of searching at random in parameter space: not elegant, but sometimes effective!

The next point to note is that 5 trees have never been shortened, despite the computation and testing of (literally) thousands of alternatives; and one other has been shortened only marginally. There is, then, some suggestion that these represent genuine Wagner trees, of actual minimum length. In any case, methods now available (branch-and-bounds techniques) should allow such trees to be determined for the first 10 data sets in the table. For the rest, however, it seems unlikely that this will be practicable in the foreseeable future - and we might remember that all but the first six sets in the table were artificially produced by breaking up larger sets. It may seem encouraging that the 14 larger sets have showed fairly regular improvement in their lengths. There is even a suggestion that for some - e.g., PODO 2 - the lengths are settling down and may now be minimal; but when one looks again at the enormous numbers of potential Wagner trees that remain untested, it is hard to be optimistic. The virtual testing of some 8×10^{12} trees for a 15 OTU data set is one thing; similar testing of, say, 3×10^{33} for the 28 PODO OTU's, is another! Indeed, one could predict, for the larger data sets and the foreseeable future, that the length of the current estimate will simply remain an inverse function of the total amount of effort invested.

The last point to be noted in Table 1 is the multiplicity of estimated Wagner trees for many of the data sets. The number ranges from 1 to 68, with mean 10 and median 6; and those currently with a single tree may well yield more upon closer scrutiny. It might seem reasonable to hope, say, that PODO 2 will eventually take the step to just one tree of length

45, replacing the current plethora of 46; but my own experience suggests otherwise. For trees on real (as opposed to integer) data, the problem seems less acute. The continuous scale of measurement ensures that one almost always finds a unique minimum length. However, the relief is pretty specious, just because there is almost always a considerable number of other trees only a shade longer than the current minimum. Considered from the aspect of maximum likelihood, the differences become negligible. And to compound this problem of choice, there is the fact that the trees competing for selection may include a considerable range of shapes. Fortunately, experience suggests that they are usually quite similar. The differences commonly reside in a small subgroup that is shuffled more or less at random; or one or two maverick OTU's jump about wildly on an otherwise stable tree.

Now, I am going to suggest that these problems are nothing but phantoms of our own making. They stem from the 'Sherlock Holmes syndrome': the idea that scientific reconstruction of phylogenies is a matter of *deduction* of some final conclusion from a set of given facts. Nothing could be further from the truth - or, indeed, less scientific. Science advances by the much less spectacular process of *inductive* inference. By an untidy, complex network of interplay between hypotheses and evidence, we work to win conclusions that are uncertain but credible. From this viewpoint, our whole set of minimum and/or near-minimum trees, plus those based on argumentation schemes, compatibility cliques, monothetic subsets, ordinations, phenograms, etc., constitute *evidence*, not conclusions. They represent various patterns discernible in the data, generated by the evolutionary process and therefore, each in its own way, evidence of evolutionary history. To reconstruct that history then requires judicious consideration of all that evidence, for recent *and* fossil taxa, along with the known properties of the various synoptic devices. The aim is to produce a consistent, credible synthesis, by the application of scientific common-sense.

Let me conclude by outlining a few of the things we can do towards such a synthesis.

- (1) It is a fair hypothesis that a set of minimum or near-minimum trees will be roughly isomorphic with the true phylogeny: and so should some elements of phenograms, etc. If so, some groupings should be 'robust', in the sense that they turn up in all or most observed patterns. If found, such groups are strong contenders for monophyletic status (in whichever version applies). We have, too, some excellent numerical methods for seeking such groups and estimating robustness, via consensus trees and component frequencies (see Penney et al 1982 for an example).
- (2) We can examine the lengths of branches on trees, and the 'moats' on phenograms. Usually, some will be much longer than others (carry a greater number of inferred apomorphies or imply greater phenetic isolation). It is then fair to regard the large ones as, in some reasonable sense, more 'significant', and the groups that they delineate as more credibly monophyletic (suitably construed). By progressively deleting the shorter internodes from a dendrogram, one can display the broader, more significant structure - and perhaps, groups that are usefully robust, even if not fully resolved.
- (3) Ordinations, phenograms and similarity matrices can provide evidence of compact, isolated, and credibly monophyletic groups, e.g., the 'ball-clusters' of Jardine et al (1969). Moreover, observed phenetic structure should be compatible with (explicable by) cladistic structure.
- (4) We can regularly examine the credibility of the implied evolution of character states. Dollo's Law, for instance, is hardly a Divine Commandment; but there can be cases where its contravention would be incredible. It might also be worth examining implied *rates* of evolution for their general credibility.
- (5) If inconsistencies persist and/or credibility is slow to appear, we should not hesitate to reexamine our data. Although gathered with care, they are themselves theory-laden and never

beyond judicious, responsible revision. And it is just the process of studying the evidence that can generate such revision.

(6) Finally, we can give up worrying if our more credible conclusions still yield an incompletely resolved dendrogram. Unless committed to the ultra-Hennigian nonsense, of having no more than 2 members in each taxon, an unresolved group causes no real problem. It illustrates the plain, scientific fact, that the 'grain' of our data may be too coarse to provide a clearer picture.

That is no doubt a poor and incomplete list. It represents a tentative glance at an area of study that is relatively unworked, but, in my opinion, one of crucial importance. I also believe that it is the one now most ripe for advances in theory and technique.

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TABLE 1. Lengths of estimated Wagner trees for 24 data sets (see Rohlf et al 1983b) as given by various methods (see text).

DATA SET	MICKEVICH (1978)	WAGNER78	ROHLF et al, A	ROHLF et al, B	SWOFFORD	NWAG+
MENID, 1	50	50	50(11)	50(12)	-	-
2	82	82	81(10)	81(24)	-	-
CATOS, 1	21	21	21(5)	21(12)	-	-
2	62	56	56(1)	56(1)	-	-
DIPOD, 1	90	97.2	96.9(1)	96.9(1)	-	-
2	110	110	110(10)	110(15)	-	-
PAP1, 1	398	399	384(1)	384(1)	-	-
2	245	247	243(1)	239(1)	-	-
PAP2, 1	367	357	353(1)	353(5)	-	-
2	222	227	223(3)	223(18)	-	-
AED1, 1	422	415.0	410.2(1)	410.2(1)	409.8(1)	409.9(2)
2	456	465.7	459.7(1)	459.7(1)	455.4(1)	455.4(1)
AED2, 1	380	375.5	370.5(1)	370.5(1)	370.4(1)	370.0(1) 369.5(1)
2	427	426.6	422.3(1)	420.9(1)	420.0(1)	419.9(1)
PODO, 1	112	113	111(10)	111(21)	-	-
2	46	47	46(10)	46(68)	-	-
HOP1, 1	298	306	299(2)	298(4)	297(5)	297(9)
2	530	485	482(1)	482(3)	480(10+)	480(1)
HOP2, 1	311	305	300(1)	300(4)	-	300(8)
2	454	472	467(3)	467(5)	464(1)	466(13)
HOP3, 1	317	313	306(2)	306(2)	-	306(13)
2	463	457	451(1)	451(1)	448(4)	448(6)
HOP4, 1	333	303	301(3)	301(5)	300(4)	300(4)
2	402	455	445(1)	444(7)	443(10+)	442(6)

Abstracts from Cladistics, Systematics & Phylogeny Symposium

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PRESENTED PAPERS

MITCHELL'S THEOREM AND ITS IMPACT ON BIOLOGY

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Cladistics is concerned with the recognition of clades, i.e. "monophyletic groups". It thus assumes that evolution has occurred. On the basis of further assumptions, the recognition of clades can be only by the occurrence of advanced characteristics, in the evolutionary sense, in each clade. This has the standing of a theorem in an axiomatic system. Branching systems, or cladograms are used to depict the relationships between clades; these are not phylogenetic trees. That the assumptions are not entirely justified is clear from obtaining different results using different characters. Some choice or compromise is necessary. The cladograms using combinations of such incongruent characters are formed on the basis of the least number of evolutionary changes with or without restrictions on this criterion, i.e. tree parsimony. Other parsimony requirements are not usually considered. Still further problems arise in establishing primitive and advanced states of attributes and in establishing homologies. Moreover all cladograms of taxa above the species level will be more or less distorted since phylogenetic branching takes place at the species level.

The conversion of cladograms into practical systematic arrangements is surrounded with problems. Nevertheless clades can often clearly be recognized by these methods and, when discussing historical processes, it is clearly the clade, a result of evolutionary processes that must be the basis for our discussion.

PACIFIC BIOGEOGRAPHY

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According to Croizat's global synthesis, the main biogeographic patterns include amphi-Atlantic, amphi-Pacific, amphi-Indian Ocean, and bipolar. Geological/geophysical theories vary, but agree that sea-floor spreading in the Pacific is different in its effect from that in other ocean basins. The difference allows for radial expansion of the basin and not merely east-west displacement of continental areas. Biogeographic data suggest that bipolar distributions are to be reckoned among the results of sea-floor spreading in the Pacific. Data from one group of inshore fishes (family Engraulidae) exemplify this notion and add, as terminal parts of the differentiation of the Pacific basin, trans-Panamanian marine vicariance and a collateral occurrence in freshwater of tropical South America.

THE WAGNER OLYMPICS: SHORT IS BEAUTIFUL

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In common usage, "cladistics" may refer to any of three different things: (a) the ordering of taxa, typically on a dendrogram (cladogram), in a way that provides an estimate of their phylogeny; (b) the use, when constructing such a dendrogram, of inferred polarities of character state sequences; (c) the construction of a classification that takes its structure entirely from such a dendrogram. It is important to realise that numerical cladistics is essentially concerned only with the first; the second (inferences as to primitive and derived states) need enter only when it comes to placing a root on the tree.

A popular form of numerical cladistics involves the computation of "Wagner" trees. These are purely mathematical objects, but can be interpreted in various ways. In one version, they display similarity relations of a particular kind: the most economical way to change any OTU at a terminal node into each of the others via a branching network. In the most popular version, they are unrooted cladograms, to which a root can be attached by various methods (outgroups, inferred ancestors, etc.). Under the latter interpretation, many folk have come to believe that an actual or estimated Wagner tree directly provides the best possible estimate of phylogeny. There are problems in this attitude, as illustrated by the history of 24 data sets that have been intensively studied over the past few years. A few sets have consistently yielded the same tree, over and over; but others have from time to time yielded a shorter tree than the current one and/or several of the same length. Indeed, with sizeable data sets there is no way of knowing whether a tree is really unique or really of minimal length. Also, what significance should we attach to the fact that one tree is, say, 0.1% shorter than another?

The notion that the 'true' Wagner tree will reveal to us the correct interpretation of our data thus becomes suspect, even paradoxical. The problem vanishes if we can accept that Wagner trees - and phenograms, ordinations, compatibility cliques, and the rest - all seek to display patterns that were generated in our data by an evolutionary process. Insights into the nature of that process, or the actual history of a particular group, can only come from careful evaluation of all the data to yield a solution that is consistent and therefore credible. To that end we can, for instance, seek 'robust' groups, which appear in many kinds of pattern; or 'significant' groups, which are vouched for by many characters. We can examine the credibility of implied routes and rates of character-change, and even the credibility of our data! Nor should we worry too much about incompletely resolved cladograms. The grain of our data may never be fine enough to provide a picture that is both clear and accurate!

DISTANCE WAGNER PROCEDURES AND THE ESTIMATION OF MOST
PARSIMONIOUS TREES

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The distance Wagner algorithm (Farris 1972) was developed as an extension of the Wagner algorithm (Farris 1970) for use on distance matrices without reference to character data. Both methods have since been widely used in phylogenetic analysis. However, the relationship between these two methods remains somewhat obscure. Although the goals of the two procedures seem to be presented in the recent literature as quite different, the distance Wagner method, like the Wagner method, may be regarded as a method for estimating most parsimonious trees. With this perspective, the ability of the distance Wagner algorithm to estimate most parsimonious trees is examined in this paper and a possible alteration to the algorithm is suggested which may produce improved estimates. This new algorithm is compared to the original distance Wagner algorithm and to the basic Wagner algorithm in simulations.

CLADISTICS AND THE FUNNEL-WEB SPIDERS

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On a cladogram of funnel-web, trap-door, and tarantula spiders of the world, two possibilities of the relationships of the Australian funnel-web spider genus Atrax are evident. Initial examination of the data suggests that Atrax belongs to the "high-headed burrowers", the Fornicephalae but upon attempting to incorporate the genus into one of the families of that micro-order from 6-11 additional steps are needed. In contrast, despite initial evidence to the contrary, Atrax requires fewer steps to be included in the hexathelid Tuberculotae. The analysis could not operate without a falsifiable cladogram of the infra-order but will be tested by a cladogram of the species of Atrax.

A PREDICTIVE CLADISTIC PHYLOGENY FOR THE BORONIEAE (RUTACEAE)

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The tribe Boronieae, as circumscribed by Engler (1896, 1931), consisted of 19 genera arranged within five subtribes. Two genera have since been synonymised (Pleurandropsis under Urocarpus and Rossittia has been shown to be a lepidote species of Hibbertia Andr.), and five others have been either reinstated (i.e. Drummondita and Urocarpus) or newly described (i.e. Muiriantha, Neobyrsesia and Rhadinothamnus). Since Engler's time, taxonomic revisions of only five genera of Boronieae have been published:

viz. - Acradenia (Hartley 1977), Correa (Wilson 1961), Crowea (Wilson 1970), Eriostemon (Wilson 1970) and Phebalium (Wilson 1970), although semi-revisionary information is available for the genera endemic in Western Australia (Wilson unpublished ms.) and a revision of Zieria is nearing completion (Armstrong, unpublished data).

Apart from the subtribal classifications proposed by Mueller (1855, 1859, 1862), Bentham (1863) and Engler (1896, 1931), few authors have attempted to assess the taxonomic affinities of the genera in the tribe. Smith-White (1954) suggested a phylogenetic scheme for the Boronieae based almost entirely on chromosome numbers and Wilson (1970) presented an account of the generic affinities in the subtribe Eriostemoninae. To date, no comprehensive interpretation of phylogenetic relationships, based on an extensive assessment of comparative morphological data, has been presented. My primary aim in this paper is to establish the most plausible phylogeny for the tribe and to compare this hypothesis with the subtribal classifications proposed previously.

Since the sister group of the Boronieae could not be determined with any degree of confidence a preliminary cladistic analysis of the Australasian genera of Rutaceae was undertaken. This revealed that the genera Acradenia and Zieridium were misplaced in Boronieae, and it suggested that three additional genera (Brombya, Euodia sens. strict. and Medicosma) should be included in the tribe. This preliminary analysis of relationships provided a means of determining character transformation series and rooting the various branching diagrams produced in the subsequent analyses.

The Boronieae were analysed cladistically using various computer programs (ten in all); each method is contrasted, the assumptions inherent in each program assessed and their known limitations discussed. Colless's NWAG method, combined with his global branch-swapping program NSWAP, produced the shortest trees, 16 in all! They suggested that "Aff. Bouchardatia" (i.e. Hartley's 'Melicope erythrocoeca group') is the sister taxon to the Boronieae. Moreover, Eriostemon and Phebalium are, at best, paraphyletic and arguably polyphyletic: Crowea and Eriostemon sect. Eriostemon form a monophyletic group, as do Microcybe and Phebalium sect. Phebalium, Nematolepis and Phebalium sect. Eriostemoides, Philotheca and Eriostemon sect. Nigrostipulae, and Rhadinothamnus and Phebalium sect. Gonioclados. Asterolasia is congeneric with Urocarpus, which is closest in affinity to Phebalium sect. Leionema.

A revised classification of the Boronieae, derived directly from the phylogenetic analysis, is suggested. In addition, the cladistic hypotheses will be compared with the known biogeographical patterns of the Boronieae and inferences made about the historical biogeography of the tribe.

A CLADISTIC AND BIOGEOGRAPHIC ANALYSIS OF THE AMERICAN FRANKENIAS

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The family Frankeniaceae has an interruptedly cosmopolitan distribution, occurring in dry climatic regions on all five continents. Most species belong to the genus Frankenia. The only existing classification of Frankenia, that of Niedenzu (1895, 1925), is both out-dated and artificial, and critical

revisionary studies are clearly needed. Results of such a study of the American frankenias are discussed. These 14 species, all woody perennials, are widely distributed in dry temperate and subtropical zones of North and South America. They differ markedly in soil preference with different species favoring saline, saline-gypseous, or well-drained gypsum soils. A cladistic analysis of 16 morphological characters was performed to examine relationships among species. The cladistic procedure used is the Unrooted Wagner Network Method of Farris *et al.* (1970) with the network subsequently rooted. Determination of appropriate outgroups for assessing directions of character evolution in *Frankenia* is difficult. Two different approaches for determining character state polarities are discussed and the resulting cladograms compared. Characters are polarized using outgroup analysis with the small genus *Hypericopsis* (Frankeniaceae) as a provisional outgroup and on the basis of comparisons with other families in the Violales. In the latter case, for a given character the state considered to represent the generalized condition in the Violales is recognized as plesiomorphic in *Frankenia*. These analyses and other evidence support the interpretation that the altiplano species, *F. triandra*, and the four Patagonian species form a closely related species alliance and that the four North American species, *F. jamesii*, *F. palmeri*, *F. gypsophila*, and *F. margaritae*, also represent another closely related species group. The former are all halophytes, whereas the latter, with the exception of *F. palmeri*, are gypsophiles. Cladistic analyses and other available evidence also suggest that several long-range disjunctions involving closely related species have occurred.

THE CLAX SYSTEM OF PHYLOGENETIC ANALYSIS - WHAT AND WHY

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The CLAX system, for which the programs (in Pascal) are now being de-bugged and polished by Christopher S. Johnson, is intended for use in an avowedly phylogenetic context - we regard transform cladistics as a sterile aberration. CLAX is a top-down procedure (i.e. grouping the most synapomorphic taxa first) with user-control of the admission of character-state reversibility, as well as user-choice intervention at intermediate stages in the analysis for large taxon- and character sets.

It is designed to avoid most of the pitfalls of the usual "most-parsimonious" approaches (such as Farris's Wagner procedures): (1) such methods frequently fail to find a shortest tree, (2) there may be very many shortest trees of which they find one or two at most, (3) there may be an even greater number of supraminimal trees longer by only one to two steps which are worthy of consideration since variants, whether minimal or supraminimal, may differ greatly from each other in topology, (4) shortest trees in practice tend to involve numerous and often repeated reversals of character-state change, (5) shortest trees (and supraminimals) may involve postulating functionally impossible intermediate hypothetical ancestors and are therefore not necessarily parsimonious at all in the sense of minimising assumptions necessary for "explanation" in a wider context.

In particular, CLAX seeks partial trees of supraminimal length (longer by one or a few steps, as determined by the user), both in seeking all minimals and for consideration of supraminimals themselves.

While CLAX primarily performs no-reversal analysis with user-determined character-state polarity, CLAXMIN is a development to permit reversal, no-reversal, controlled reversal, and unrestricted reversal. CLAX methods have been used with success on Myrtales (19 taxa - families or groups of doubtful position - with over 70 characters), Myrtaceae, and the eucalypts, both in comparison and conjunction with other approaches. CLAX has revealed more minimal trees than those other methods and has permitted detailed evaluation of partial trees and search for "most robust" segments of trees.

We plan to apply it to various other taxonomic groups in the near future.

A REAPPRAISAL OF NELSON'S DIRECT METHOD OF CHARACTER ANALYSIS

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Outgroup comparison, the method most commonly used in cladistic analysis for polarizing character transformation series, requires the existence of a higher level cladistic classification. Such higher level classifications themselves may be based on outgroup comparisons. Therefore, a technique of character analysis that is independent of existing classifications is needed to provide starting points for cladistic analysis. Nelson's "direct method" is such a technique. It uses the observed relationship of generality shown by homologous character states in an ontogenetic transformational sequence to provide a most parsimonious character phylogeny (character x is more general than state y if it is possessed by all of the species that have state y and by some that do not as well). As presented initially, this method was based on the type of transformational sequence most commonly found in vertebrate ontogeny: the unique, irreversible, linear development of a particular organ through a succession of stages. The logic of Nelson's method may be extended however, to cover non-linear, reversible, and non-unique ontogenetic sequences and can be applied in the analysis of ultrastructural characters that have no observable ontogeny. All that is required is that an unequivocal relationship of generality exists between homologous character states. Some novel applications of this method are discussed, including some examples from higher plants. In particular, the "classic" botanical example of ontogenetic recapitulation, Acacia leaf development, is examined critically. The significance of the order of appearance of character states in development is discussed with respect to the different types of transformational sequences.

RELATIONSHIPS WITHIN THE STRINGYBARK EUCALYPTS OF EASTERN AUSTRALIA

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The stringybark eucalypts (Eucalyptus informal subgenus Monocalyptus) form a monophyletic group characterized by seedling hairs. The group includes the informal series Capitellatae and Olsenianae.

On average five trees from each of 32 populations were sampled from as far north as the Atherton Tablelands Qld, through N.S.W., Vic. and S.A. Seedlings were raised from three parent trees per population.

Phenetic methods of classification, based on 41 adult characters and 26 seedling characters, were used to define terminal taxa; the results generally confirmed the taxa recognized by others, although E. tindaliae and E. phaeotricha (including the Atherton population) were equivalent, and E. deformis (= E. oblonga subsp. oblonga) and E. capitellata differed in only a few characters. The degree of dissimilarity between some other pair of taxa raised the problem of taxonomic rank, but this did not affect the following analyses.

The pattern of relationships between the terminal taxa was analysed firstly by methods of tree generation based on distance matrices. A minimum spanning tree (MST), which linked first neighbours, placed one or two taxa in odd positions. An additive similarity tree (ADTREE) produced an unrooted tree of best fit to the initial distance matrix. The cladistic methods of character compatibility (CLIQUE) and parsimony (WAGNER) were also applied after recoding characters to binary states. Some trees were rooted by outgroup comparison, the outgroups being subgenus Idiogenes and series Acmenoideae. ADTREE proved useful because it provided a very similar answer to those based on cladistic methods, but was less limited by the number of taxa and characters, and did not require the recoding of characters as transformation series.

The consensus tree suggests that E. muelleriana is close to the root, and that there are five major lineages:

1. olsenii, baxteri (2 subspecies), alpina (2 species)
2. youmanii, laevopinea, macrorhyncha, cannonii
3. deformis, capitellata, camfieldii, sp. nov.
4. blaxlandii, agglomerata, cameronii, globoidea
5. conglomerata, eugeniodes, mckieana, oblonga, ligustrina, sp. nov.

E. tindaliae and E. caliginosa are near the stem of the tree.

LUNGFISH, CLADISTICS AND THE DETERMINATION OF SYNAPOMORPHIES

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Campbell and Barwick (1983) distinguish two forms of dipnoan dentition: those with a shagreen of denticles that are shed during growth; and those with large dentine covered surfaces that are added to during growth. An application of the outgroup rule, evidence from ontogeny and the most parsimonious interpretation of Miles' (1977) phylogenetic data suggest that the former, a shagreen of denticles, is the primitive dipnoan dentition. However a functional analysis of the dentitions and associated feeding mechanisms suggest that a shagreen of denticles is highly advanced. The functional data in conjunction with stratigraphic data suggest that large dentine covered surfaces is the primitive condition. The conclusions of the functional analysis are favoured. The attempt to determine the polarity of the dipnoan dentition morphocline points to the dangers of treating

characters as isolated entities, independent of functional and developmental constraints. The functional analysis implies that the shagreen of denticles present in dipnoans is not homologous with those of other gnathostomes and hence that the outgroup rule is not applicable in this case. A close examination of the ontogenetic evidence reveals that the ontogenetic data reflects developmental constraints, not ancestry. Campbell and Barwick's analysis of dipnoan dentitions renders Miles' parsimony argument invalid.

POSTER PAPERS

A REANALYSIS OF KLUGE(1976) 'PHYLOGENETIC RELATIONSHIPS IN THE LIZARD FAMILY PYGOPODIDAE'

K. DAY

Division of Water and Land Resources, CSIRO, G.P.O. Box 1666, Canberra A.C.T. 2601

Kluge states that his data set consists of the more conservative osteological characters in the pygopodid phenotype. His data were reexamined to determine the effect of reduced conservativeness on the cladistic path. The Wagner trees generated by the full data set differed markedly from that calculated by Kluge. Reduced conservativeness resulted in the formation of new clades and a higher number of possible trees at each level.

Kluge, A.G. (1976). Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. Misc. Publ. No. 152. Museum of Zoology, University of Michigan.

A MODEL OF IMMUNOLOGICAL DISTANCES IN SYSTEMATICS

D.P. FAITH

Division of Water and Land Resources, CSIRO, G.P.O. Box 1666, Canberra A.C.T. 2601

While immunological distances among taxa have had wide use in systematics, there has been some doubt about their utility because of the observed non-metricity of such distance matrices. A model is presented here relating observed immunological distance to the actual number of antigenic site differences between taxa. This model accounts for the observed departures of these distances from the metric conditions of reciprocity and triangle inequality. Based upon the model, two procedures are suggested for the transformation of immunological distances to metric distances appropriate for phylogenetic analysis. The model implies that the usual scaling adjustments applied to the immunological distance matrix are inappropriate; however, the same transformation applied instead to an initial similarity matrix will solve a scaling problem. Non-reciprocity of the distances is shown to remain a problem independent of this initial scaling problem.

PHYLOGENY OF PARAHEBE CATARRACTAE AND RELATED SPECIES
(SCROPHULARIACEAE)

P. GARNOCK-JONES

Botany Division, DSIR, Christchurch, New Zealand

4 taxa previously treated as subspecies of Parahebe catarractae have been studied in a simple cladistic analysis along with 4 other species. Together these 8 entities constitute a monophyletic group defined by 2 synapomorphies.

The basic features of the cladogram are:

1. The primary speciation event in the group resulted in a North Island species and a South Island species, the ancestors of the 4 taxa present on each island today. Thus the 2 North Island subspecies of P. catarractae share a more recent ancestor with P. hookeriana and P. olsenii than they do with P. catarractae s. str., and should be treated as one, or two, distinct species.
2. In the South Island, P. decora, P. lyallii and P. catarractae share an immediate ancestor not shared with P. catarractae subsp. martinii. Thus the latter should also be accorded species rank.
3. Similarities between P. catarractae, P. "martinii" and P. diffusa in flower size and colour and in leaf size and toothiness are now considered likely to be symplesiomorphic and thus do not imply that these species constitute a clade. The idea that P. catarractae sens. lat. as studied by Garnock-Jones and Langer (1980) represents the plesiomorphic parts of this species complex is supported by recent biogeographic considerations.

Thinking cladistically has helped to resolve a situation where the basic taxa had been recognised by phenetic methods applied at the population level, but ranks had been incorrectly applied to them. Further refinements of this phylogeny will probably be biogeographically illuminating, and provide some evidence concerning rates of speciation in the complex.

FAUNAL CLADISTICS AND MONTANE RAINFOREST REFUGIA: A
NORTHEASTERN QUEENSLAND CASE STUDY

M.N. SCHUSTER

Department of Administrative Services, Canberra

Phylogenetic analyses were undertaken on the montane rainforest scincid fauna of northeastern Queensland.

Altitudinal zonation of the scincid assemblages was found to be related to the relative age of each grouping.

Leiopisma sp. (Mt Bartle Frere), a Gondwanic relictual form, is restricted to the 1400-1622m (cool temperate) zone of Mt Bartle Frere. An upland temperate group (genus Lampropholis), of probable Miocene origins, is confined to the 1050-1400m forest zone. Another scincid assemblage, of more recent (possible Pleistocene origins) is confined to the lowland tropical forest zone.

Biogeographic conclusions, with reference to rainforest refugia history, are also given.

CLADISTIC ANALYSIS OF THE MOSS MACROMITRIUM IN AUSTRALASIA

D.H. VITT

Department of Botany, University of Alberta, Edmonton, Canada

H.P. RAMSAY

School of Botany, University of New South Wales, P.O. Box 1, Kensington, N.S.W. 2033, Australia

The moss Macromitrium with over 450 names attributed to the genus, is one of several tropical and sub-tropical genera in the family Orthotrichaceae. Macromitrium species have proved very difficult to interpret taxonomically in the past. The use of numerical techniques have enabled us to arrange the specimens from the Australasian region (Australia, New Caledonia, Norfolk Island, Lord Howe Island and New Zealand) into 34 taxa from 95 names. Two segregate genera are recognised, Macrocoma and Groustiella, each with a single species in the region. The other 32 taxa are species of Macromitrium one with two subspecies. A data matrix for 30 characters the states of which have been classified as plesiotypic or apotypic based on generalised ex-group comparison has been formed. In this case a generalised Bryalean moss (diplolepideous, acrocarpous) is used (sensu Vitt 1982) as relationships for the Orthotrichaceae are not clear.

The reconstructed phylogeny presented as a Wagner divergent ground plan and as a Cladogram separates taxa into 7 Groups. Distribution and chromosome data have been added to this. The major patterns of distribution of Macromitrium in the region are Australian, and New Zealand endemics, species occurring in both regions and those with extended distribution e.g. to New Caledonia. The Australian species can be divided into those with primarily tropical and those with primarily temperate distribution.

The limitations of working with a small number of the total taxa in a portion of its geographic range is illustrated by the numbers of parallelisms and numbers of apotypic character differences between some related taxa.

A tentative study of some New Guinea forms shows these to be unrelated to the Australian groups as understood at present, thus emphasising the limitations of the data set used in terms of total understanding of the genus.

CLADODODISTICS

J.G. WEST

Division of Plant Industry, CSIRO, G.P.O. Box 1600, Canberra A.C.T. 2601

Dodonaea is a predominantly Australian genus of the family Sapindaceae. Sixty-one species occur in Australia one of which, D. viscosa, extends beyond Australia with a pantropical distribution and with extension to

southern Africa and the Pacific. About 6 other species all showing morphological features very similar to D. viscosa occur in tropical areas outside Australia. Within Australia the genus exhibits great morphological variability and in its Australia-wide distribution occupies a vast range of habitat types. A critical morphological revision of the genus in Australia has just been completed; the previous classification of Radlkofer (1933) being outdated and artificial. Cladistic analyses have been performed using varying combinations of 26 morphological characters to assess phylogenetic relationships of the 61 species. Character polarizations were determined largely by the outgroup method using the tribe Dodonaeae as the outgroup. In each analysis the shortest trees contain the same or very similar robust groups of species. The Wagner tree constructed when using all 26 characters shows these fairly distinct groups. However, this cladogram, like most of those produced, contains a high percentage of homoplasy (c. 80%) and it is obvious that many characters are unresolved; both reversals and parallelisms occur throughout. Detailed consideration of the biological meaning of some of these homoplasies and the fact that some taxa are variable for some character states enables acceptance of some of these reversals and parallelisms and contributes to the understanding of some of the characters, while others remain unresolved. Comparison of the morphological and ecological diversity and the geographic distribution of species belonging to the 7 groups (as shown on the maps) emphasises the distinctness of the groups and provides some insight into speciation events that may have occurred within the genus in Australia. This unresolved cladogram highlights some of the inherent problems encountered when trying to determine the most plausible phylogeny for a relatively large number of taxa at the species level with a relatively small number of morphological characters only. One suggestion for this lack of resolution may be that we just don't have enough data or information at this stage to resolve the situation. Another explanation is that this group is in an active phase of radiation, a process in which you might expect a high degree of homoplasy. This hypothesis is consistent with my earlier proposal that those Dodonaea species occurring in the arid regions of Australia are the result of relatively recent invasions.

A PRELIMINARY CLADISTIC ANALYSIS OF THE METROSIDEROS SUBALLIANCE (MYRTACEAE)

P.G. WILSON & P.H. WESTON

National Herbarium of New South Wales, Royal Botanic Gardens, Sydney
N.S.W. 2000

The Metrosideros suballiance is one of four subgroups of the Metrosideros alliance recognised in Briggs and Johnson's (1979) classification of the Myrtaceae. This group could prove to be paraphyletic however, as it is not defined by any known synapomorphy. Moreover, generic limits within this group have been the subject of contention, Dawson (1976) maintaining three genera and Briggs and Johnson suggesting nine. The aim of this analysis is to clarify the relationships of the species within the group and to assess the group's integrity. Twentyone morphological characters were used to construct Wagner networks linking twenty terminal taxa (species and species groups). Apomorphous states of fifteen of the characters could be postulated confidently on the basis of outgroup comparisons, thus limiting the number of alternative rooted Wagner trees. The data were analysed using Wagner-78 with one input sequence. Equally parsimonious alternative topologies were produced manually by plotting alternative character

distributions and swapping branches. These preliminary results cast doubt on all previously proposed classifications. In particular, *Metrosideros* (sens. Dawson) and *Mearnsia* (sens. Briggs and Johnson) appear to be paraphyletic no matter where the networks are rooted. A number of other previously recognised taxa however, appear to be monophyletic.

Report from the Bureau of Flora and Fauna

Volume 4 of the *Flora of Australia* is with Griffin Press and should be printed in September. Volume 25 is being refereed, while preliminary editing of Volume 46 and 45 has begun.

The new Guide for Contributors was published in August. Copies are being sent to all who have agreed to contribute to the Flora, as well as the major Australian herbaria. Further copies are available on request.

The ABRS Advisory Committee will meet from 11 to 13 September to consider applications for grants in 1985. Ministerial approval of recommendations should be received by mid October.

A reorganisation of Bureau staff is currently in progress. Alison McCusker has been appointed Assistant Secretary of the Environment Strategy Division in the Department. Roger Hnatiuk has moved to the position of Assistant Director, Flora Section, and Alex George and Helen Hewson revert to Executive Editor (*Flora of Australia*) and Botanist, respectively. Geetha Sriprakash, who has acted as Editorial Assistant since December 1983, has taken a position in the Department of Resources and Energy. The position of Editorial Assistant (Science 2) will probably be filled on a permanent basis and is expected to be advertised shortly.

Alex George
Executive Editor

Symposium

The next General Meeting of the Society will be held on Tuesday 12 February, 1985 in conjunction with a symposium on alpine biota to be held at Thredbo, New South Wales (see insert in previous issue).

Council is anxious that the overall program has a scope which is of interest to all members of ASBS. Council is therefore interested in organizing a session of contributed papers on general or specialized topics in systematics which might be held in conjunction with, but independent of, the Alpine Symposium.

Any one interested in presenting a paper is asked to contact Judy West, Australian National Herbarium, G.P.O. Box 1600, Canberra, A.C.T. 2601.

The symposium on the Origin and Evolution of Australasian Alpine Biota will be held on 11-12 February 1985. There is still accommodation available at Thredbo. For further information and enrolment forms contact Bryan Barlow (062) 465904 or Max Gray (062) 465914, Australian National Herbarium, G.P.O. Box 1600, Canberra, A.C.T. 2601.

Chapter News

ADELAIDE CHAPTER

A programme of regular evening meetings, occasional lunchtime seminars and weekend excursions has been enjoyed by members, who have attended in moderate to low numbers.

- FEBRUARY 29 - Flora research at Black Hill. Dr R. Williams, Black Hill Native Flora Park.
- MARCH 28 - Visitors in a dreamtime land: botanical exploration of north-western South Australia. Kathie Stove, State Herbarium.
- APRIL 18 - Practical aspects of maintaining a computerised literature index. Russell Cook, Waite Institute.
- APRIL 19 - Lunchtime talk on Banksia. Alex George, Bureau of Flora and Fauna. Alex kindly gave this talk in lieu of a planned visit to the Griffin Press to view printing of the Flora of Australia. The visit was cancelled for security reasons.
- MAY 13 - Picnic at Black Hill Native Flora Park with inspection of nursery, wildflower garden, visitor centre and a self-guided nature trail walk.
- MAY 30 - Botanical awareness in the community - educating future generations. Tony Sadler, Education Officer, Botanic Gardens of Adelaide.
- JUNE 27 - A splitter's guide to the Australian Acanthaceae. Robyn Barker, State Herbarium of South Australia.
- JULY 25 - The impact of shipping on the invasion of Norway by alien plants. Prof. Torre Ouren, Geographical Institute, Bergen, Norway.
- AUGUST 29 - The taxonomy of *Eucalyptus* Series *Dumora*: coping with morphological variation. Dr Peter Lang, Department of Environment and Planning.

Further meetings are planned for September 10 and 26, October 13 (excursion) October 31 and November 28.

L. Haegi
Convener

MELBOURNE CHAPTER

For our June meeting Ian Pascoe, Victortian Plant Research Institute, spoke on "Development of a national mycological collection".

Ian discussed the history, current status and future directions of mycological herbaria in Australia.

Daniel McAlpine established Australia's first mycological herbarium in Melbourne in 1890. After McAlpine's retirement in 1916, interest in taxonomic mycology in Australia waned and the existing herbaria were neglected. Apart

from Cleland and Hansford in South Australia during the 30's, 40's and 50's very little serious taxonomic mycology was done and very little material added to existing herbaria until the 60's and 70's. The majority of mycological specimens in Australia are lodged in about 6 herbaria but only half of these have active taxonomist/curators working with them.

At the July meeting Don Foreman, National Herbarium of Victoria, spoke on "The Monimiaceae - A Key family to the understanding of the Laurales".

Recent evidence obtained from the fields of wood anatomy, reproductive morphology, anther and pollen development, and pollen morphology (including exine ultrastructure) indicate that the family Monimiaceae (s.l.) is a far more heterogeneous assemblage of plants than had previously been recognized.

It has been suggested the family could be split into a number of smaller more homogeneous families. This is contrary to the ideas of workers such as Thorne, Dahlgren, Cronquist and Takhtajan who in their current systems of classification of angiosperms all treat the Monimiaceae (including the Atherospermataceae) as a single family divided into varying numbers of subfamilies.

Studies of Australian taxa supports the suggestions by workers such as Schodde that the Atherospermataceae should be recognized as a distinct family from the Monimiaceae. An increasing amount of evidence suggests that most of the currently recognised sub-family segregates should also be recognised at family level.

In August, Michael Looker, National Herbarium of Victoria, gave a talk on "The Living Collections Division of the Royal Botanic Gardens, Kew, Great Britain - its layout, management and modern uses".

Barry Conn

Letters to the Editor

PHYLOGENY OF THE EUCALYPTS

In reference to the letter of Dr L.A.S. Johnson (ASBS Newsletter 39: 25-28, June 1984), I must agree with many of the points that he makes, particularly with regard to the rejection of the overly-emotional reactions to the split in *Eucalyptus*. I also acknowledge that his classification is a defensible extension of his phylogenetic reconstruction. I also respect the importance of his classification at the various hierarchical levels within the major groups. However, I am forced to reply to his sweeping dismissal of Ladiges and Humphries (1983).

It is unfortunate that at this stage the paper of Johnson and Briggs, which analyses the Myrtaceae in depth, is still in press. It makes it difficult for all to judge the basis of Johnson's final phylogenetic interpretation of the eucalypts (and hence the proposed taxonomic revision) and to judge the differences in our data sets and methodology. Nonetheless, given that we have exchanged and discussed (ours in particular) draft manuscripts, and that he utilised some of our data matrix in his latest numerical analysis to present a result different from that which he presented at the Botanical Congress (1981), I am disappointed that he describes our work as "erroneous, incomplete and unbalanced".

One of the main issues is the interpretation of characters or character states as evolutionary transformation series, i.e. what is the general or primitive condition and what is the advanced? Our interpretations were based on two criteria - ontogeny and the condition in the outgroup Arillastrum gummiferum. Thus given our data set, the hypothesis that Eucalyptus is monophyletic was the most parsimonious, the similarity of Bloodwoods to Angophora relating largely to the sharing of primitive characters. Based on this result, Eucalyptus is united and characterised by disjunct-opposite phyllotaxy ("alternate" adult foliage) and the development of at least one operculum. Of course the solution itself raised a number of problems, such as the need to re-examine some aspects of operculum development, and our hypothesis may prove less likely given more data.

I for one refrain from further comment until the publication of Johnson and Briggs' paper.

Pauline Y. Ladiges

Reference

Ladiges, P.Y., and Humphries, C.J. (1983). A cladistic study of Arillastrum, Angophora and Eucalyptus (Myrtaceae). Bot. J. Linn. Soc. 87, 105-34.

ASBS Council Elections

1985-1986 Term

In accordance with the Constitution of the Society, nominations are called for all positions on the Council for 1985-86 term of office: President, Vice-President, Secretary, Treasurer, 2 Councillors.

Each nominee must be proposed by two members and his/her acceptance of nomination must accompany the nomination itself. Nominations must be on the form in the back of this issue of the Newsletter or on a facsimile of that form.

With the exception of the present Secretary, Judy West, the present officers are all available for and willing to be re-elected for another term of office. Judy West has served 4 consecutive terms and is ineligible for re-election.

All nominations must be in the hands of the Secretary, Dr J.G. West, Australian National Herbarium, CSIRO, G.P.O. Box 1600, Canberra, A.C.T. 2601 by FRIDAY, 16th NOVEMBER 1984.

Ballot papers will be sent out in December and the results of the elections will be announced at the Society's General Meeting in February 1985 at Thredbo.

RECORD OF A.S.B.S. COUNCIL MEMBERSHIP

P: President; VP: Vice-President, S: Secretary; T: Treasurer;
C: Councillor; E: Editor.

Limit of term: P and VP = 2 consecutive terms; others = 4 consecutive terms. Term = period between consecutive general meetings.

	1973 -75	1975 -76	1976 -77	1977 -79	1979 -80	1980 -81	1981 -83	1983 -85
Mr J. Armstrong		C	C					
Dr B. Barlow							VP	P
Mr D. Boyland	C,E							
Dr B. Briggs								VP
Prof. R. Carolin			P	P	VP	VP		
Prof. D. Carr	VP							
Prof. T. Clifford							P	
Dr B. Conn						T,E	T,E	
Mr A. George	C	C	C	C,E	E	E		
Dr G. Guymer							E	E
Dr L. Haegi							C	C
Mr R. Henderson		VP,E	E	VP,E			C	C
Dr R. Hnatiuk						C		
Dr J. Jessop				C	P	P		
Dr A. Kanis	T							
Mr M. Lazarides		T	T	T	T			
Mr D. McGillivray	S							
Mr A. Mitchell					C	C		
Dr P. Short								T
Dr J. West					S	S	S	S
Dr T. Whiffin	P	P	VP					
Mrs K. Wilson		S	S	S	C			

N.B. Editor is included here to complete the record of Society positions even though the Newsletter Editor is not an elected member of Council.

SPECIAL COMMITTEE ON VALID PUBLICATION

The above Committee was set up following the XIII IBC in Sydney in 1981 - see Englera 2: 74-75 (1982).

I have recently been asked to take over the duties of Secretary of this Committee and to prepare a report for the next Conference to be held in Berlin in 1987.

The Committee is charged with recommending on Articles 32 to 45 of the International Code of Botanical Nomenclature, with the exception of those portions dealing with Orthography.

If anyone has any relevant comments on those sections of the Code could they please forward them to me no later than 30 November.

Arthur D. Chapman
Bureau of Flora and Fauna
P.O. Box 1383
CANBERRA A.C.T. 2601

INSTITUTE OF BIOLOGY IN AUSTRALIA

A branch of the Institute of Biology of the United Kingdom which has 17 000 members worldwide, has recently been formed in Australia. At present, there are 186 members who are individually members of some 91 biological societies in Australia. It is intended that the branch will become completely autonomous as soon as membership has built up to a viable level. The activities of the Institute of Biology in Australia will not compete with the scientific functions of specialist biological societies. The Institute sees its role as complementary to that of existing societies. The objectives of the Institute of Biology are to foster the professional status of biologists and to accredit those engaged in biological work. The Institute aims also to act as a national advocate in matters affecting the employment of biologists and to provide a national forum for publicising the views of biologists on biological topics of national or regional interest.

Members are drawn from many fields of biological activity, including agriculture, education, forestry and medicine. The Institute of Biology in Australia would like to include a representative cross-section of all working biologists in Australia. If you are interested in joining the Institute or want more information contact the membership officer Dr Neville J. Williams, Science Centre, 35-43 Clarence Street, Sydney, NSW 2000.

The Society

The Australian Systematic Botany Society is an association of over 300 people with professional or amateur interest in Botany. The aim of the Society is to promote the study of plant systematics.

Membership

Membership is open to all those interested in plant systematics and entitles the member to attend general and chapter meetings and to receive the Newsletter. Any person may become a member by forwarding the annual subscription to the Treasurer. Subscriptions become due on the 1st January.

The Newsletter

The Newsletter appears quarterly and keeps members informed of Society events and news, and provides a vehicle for debate and discussion. In addition original articles, notes and letters (not exceeding ten pages in length) will be published. Contributions should be sent to the Editor at the address given below, preferably typed in duplicate and double-spaced. All items incorporated in the Newsletter will be duly acknowledged. Authors are alone responsible for the views expressed. The deadline for contributions is the last day of February, May, August and November.

Notes

- (1) The deadline for the next Newsletter is 30th November 1984.
- (2) ASBS Annual Membership is \$13 (Aust.) if paid by 31st March, \$15 thereafter. Students (full-time) \$10. Please remit to the Treasurer.
- (3) Advertising space is available for products or services of interest to ASBS members. Current rates are \$30 per full page, \$15 per half page. Contact the Newsletter Editor for further information.

Mailing List

All address changes should be sent to the Treasurer or the Editor.

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